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THE TYMPANIC STRUCTURES OF THE LEPIDOPTERA AND THE TAXONOMY OF THE ORDER

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Part XV (on the Hypeninæ and Herminiinæ) of my "Recherches sur les organes tympaniques des Lépidoptères en rapport avec la classification" (Studies of the tympanic organs of the Lepidoptera as a criterion of their classification), which appeared in 1960, completed the series begun in 1948. A short paper appeared in the *Lepidopterists' News* in 1952, in order to acquaint the readers with the progress of the investigation and with the important bearings thereof on the classification of the Lepidoptera (Kiriakoff 1952b).

Now that the study has been terminated, it may perhaps be of some interest to give a short summary of the research and of its final results regarding the classification of the groups involved. Stress should be also laid on the very important earlier work by A. GLENN RICHARDS, CHIN JEN LUH, I. GOHRBANDT, and H. SICK, not to speak of the pioneer in the field, Professor F. EGGERS. The latter had for the first time described the various types of tympanum and outlined the principal divisions of the tympanum-bearing groups. As it is now known, there are two main position-groupings of the lepidopterous typanum, viz. the abdominal and the thoracic type. While the question of a possible polyphylety of the abdominal type is still open, there seems to be little doubt about the monophyletic origin of the structure for those groups which possess a thoracic tympanum. Since I have dealt in my research with the latter only, I must refer the reader to the papers by KENNEL and EGGERS, and by GOHRBANDT on the abdominal structures. There are three main groups belonging to the abdominal category, viz. the Pyralidæ, the Geometridæ, and the Thyatiridæ + Drepanidæ, and they are now usually considered as superfamilies.

With reference to the thoracic structures, some excellent work has been done by RICHARDS (1933), who studied in some detail the North American Noctuidæ and more fragmentarily the other groups involved (Arctiidæ, Lymantriidæ, etc.). His conclusions regarding the general classification differ in many points from those dealt with here, mostly, I should think, because of the more complete later research on several groups only superficially studied in his excellent paper. On the other hand, RICHARDS' subdivisions of the family Noctuidæ seem on the whole to be quite acceptable, although he only studied the New World forms. So are the conclusions of CHIN JEN LUH (1936) concerning part of the American Arctiidæ; as far as I am aware, only an excerpt of his paper has been published.

I now return to my own work. In order to give a clear picture of what has been done, I am giving below, in chronological sequence, the essentials of the 15 parts of the "Recherches". The parenthetical dates refer to the papers cited in full in the references at the end of this review.

I. CTENUCHIDÆ (1948). Three main structures have been found: the "normal" or phalænoid type, very similar to that found in the Noctuidæ; a peculiar type with a horizontal tympanum, called the "thyretoid type"; and a much reduced structure, with most, but not all, features vestigial. GOHRBANDT (1939a) had already distinguished between these various structures; however, she refrained from making definite taxonomic conclusions. The "thyretoid" forms were later (1949a) placed in the new family Thyretidæ.

II. THAUMETOPŒIDÆ (1949b). These are shown to have the same type of tympanic structures as do the Thyretidæ and Notodontidæ. See also part XIII.

III. DIOPTIDÆ (1950a). This is another group belonging in the vicinity of the Notodontidæ. Some representatives have strongly reduced tympanic structures (subfamily Dioptinæ). The majority, with well developed, sometimes highly specialized structures, form the subfamily Josiinæ.

IV. NOTODONTIDÆ (1950b). A few Indo-Australian forms are aberrant in the shape of the scutal phragm and form the subfamily Tarsolepidinæ (scutal phragm narrow like that in the phalænoid type). The bulk possess a normal notodontoid (*i.e.*, broad and roof-shaped) scutal phragm: subfamily Notodontinæ. The notodontoid group was revised in a paper entitled "Sur la classification et la phylogénie de la superfamille Notodontoidea" (1950c). The superfamily Notodontoidea of D'ALMEIDA was broadened to include the families Thyretidæ, Dioptidæ, and Notodontidæ + Thaumetopœidæ. All the forms possessing a tympanum of the phalænoid (or noctuid) type were, then, placed in the

opposite superfamily Phalænoidea (later renamed Noctuoidea, on priority grounds). Sick (1940) had studied, in a paper that was at the time unknown to me, the family Dioptidæ, as well as a couple representatives of Thaumetopœidæ and Notodontidæ. His study was very complete (90% of the dioptid species), and he recognized 5 main structural types of the tympanum, including the vestigial one referred to above under III. He also was the first to point out the affinities between these several groups. Since he was not a taxonomist, he did not attempt to adjust the classification of the groups involved. Sick died shortly after the end of the Second World War.

V. A short paper (1950d) dealt with the aberrant structures of a few arctiid genera, both Old World and American.

VI. NYCTEMERIDÆ (1951a). The structures of this group do not differ notably from those of the true Arctiidæ.

VII. LITHOSIIDÆ (1951b). Most genera do not differ from the Arctiidæ. A few possess, however, an aberrant type of tympanum, with a complete, closed frame. A new family Endrosidæ (after the palearctic genus *Endrosa*) has been described to include such forms. Further research may disclose more genera belonging to this new taxon.

VIII. COCYTIIDÆ (1951c). This includes the single genus *Cocytia,* not differing, in respect to the tympanic structures, from the Noctuidæ.

IX. ARCTIIDÆ (1952a). Old World forms only were studied. For the American genera, *vide* the paper of Chin Jen Luh (1936).

X. HYBLÆIDÆ (1953). This small tropical group is mostly placed near the Noctuidæ. The moths lack, however, any trace of tympanic structures. Considering some other structural characters of the Hyblæidæ, they should be placed with the Tortricoidea, *i.e.* in an evolutive series that developed quite independently of the Noctuiformes.

XI. AGARISTIDÆ (1955). These are close to the Noctuidæ but possess an unmistakable degree of differentiation, *e.g.* the so-called pleural bulla, a large vesicle at the basis of the abdomen, visible from outside.

XII. LYMANTRIIDÆ (1956a). Some structures, especially the prespiracular cucullus, point towards a closer affinity with the Arctiidæ than with the Noctuidæ. A general survey of the super-family Phalænoidea (*recte* Noctuoidea) led to recognizing but two families, viz. Endrosidæ and Noctuidæ, the latter having two major divisions, one with a prespiracular cucullus (*i.e.,* the cucullus being placed before the first abdominal stigma), including the infrafamilies Arctiidi and Lymantriidi; the other with a postspiracular cucullus (*i.e.,* the cucullus being placed behind the first abdominal stigma), including the infrafamilies Noctuidi (including "Cocytiidæ") and Agaristidi.

XIII. A few Australian genera have been sometimes placed with the Lymantriidæ, sometimes with the Thaumetopœidæ. The tympanum does not differ from that of the latter group, so that the taxonomical position of the *Epicoma*-group is with the Notodontoidea (1956b).

XIV. NOLIDÆ (1958). These are usually considered as a "subfamily" of Arctiidæ. RICHARDS was the first to point out that their true affinities are with the Noctuidæ. However, he had some doubts about the position of the cucullus. This doubt I was able to remove by showing that the cucullus of the Nolidæ is postspiracular. The group should accordingly be placed near Noctuidi as a third infrafamily.

XV. HERMINIINÆ and HYPENINÆ (1960). RICHARDS had made a study of these groups and pointed out that 3 subfamilies could be distinguished therein, viz. Herminiinæ, Rivulinæ and Hypeninæ. As far as the two latter are concerned, the conclusions of RICHARDS have not been supported by my research. For instance, a double pocket IV was found to occur in all the groups indiscriminately, which made it useless as an important differential character. I accordingly placed both Rivulinæ and Hypeninæ with the "Erebine-Catocaline complex" of RICHARDS, a useful and probably natural division. On the other hand, the Herminiinæ possess (as RICHARDS indeed did find) a prespiracular cucullus, contrarily to all other "Noctuidæ", including the Rivulinæ and the Hypeninæ. The former must accordingly be removed from that vicinity and placed with the "prespiracular" division of the Noctuidæ, along with Arctiidæ and Lymantriidæ. The various conclusions reached in the above papers can be briefly tabulated as follows:

Subcohors Noctuiformes

A. (Includes the plesiomorphic sister-branch, *i.e.*, groups which do not have tympanic structures. The most important are the Zygænidæ).

B. The apomorphic sister-branch has tympanic structures present and contains two superfamilies.

Superfamily Notodontoidea (tympanum of the notodontoid type)
- Family Dioptidæ
  - Subfamily Dioptinæ
  - Subfamily Josiinæ
- Family Notodontidæ
  - Subfamily Tarsolepidinæ
  - Subfamily Notodontinæ (the Thaumetopœidæ might be excluded therefrom and placed in a distinct family or subfamily on other grounds than the tympanic structures)
- Family Thyretidæ

Superfamily Noctuoidea (tympanum of the phalænoid type):
Family Endrosidæ
Family Noctuidæ
Subfamily Arctiinæ (*Subfam. nova*: prespiracular hood)
Infrafamily Lymantriidi
Infrafamily Arctiidi
Infrafamily Herminiini
Subfamily Noctuinæ (*Subfam. nova*: postspiracular hood)
Infrafamily Nolidi
Infrafamily Noctuidi
Infrafamily Agaristidi

The above classification differs very distinctly from the usual one. However, I believe it to correspond more closely with the phylogeny of the higher Lepidoptera, because the tympanic structures undoubtedly are the most significant single set of characters that can be found in the Lepidoptera. Their complexity is extreme, yet they are surprisingly uniform in the various evolutionary lines that can be distinguished among their bearers. There is no doubt that they should be preferred to all other characters such as the wing-venation with all its inconsistencies.

To end this summary, I should like to point out that, in my opinion, all the groups where a tympanum occurs should be investigated for that structure. The classification of groups such as the geometrids and the pyralids cannot be considered as satisfactory so long as next to nothing is known about their tympanic structures. It is surprising to find that, since the times of Kennel and Eggers nobody has ever cared (with the exception of Gohrbandt who wrote a paper on the uraniid type of tympanum) to follow up the pioneer work of those two great lepidopterists. I can only hope that some student will undertake this immense but glorious task in order to bring our knowledge of the groups just referred to the level of what is now known about the Noctuoidea.

References

Eggers, F., 1920. Das thorakale bitympanale Organ der Lepidoptera Heterocera. *Zool. Jahrb.* (*Anat.*) 41: 273-376, 6 figs., pls.20-24.

Gohrbandt, Ilse, 1939a. Das Tympanalorgan der Syntomiden. *Zool. Anz.* 125: 23-29, 4 figs.

....., 1939b. Ein neuer Typus des Tympanalorgans der Syntomiden. *Zool. Anz.* 126: 107-116, 5 figs.

Kennel, J. v., & F. Eggers, 1933. Die abdominalen Tympanal-organe der Lepidopteren. *Zool. Jahrb.* (*Anat.*) 57: 1-105, pls.

Kiriakoff, S. G., 1948. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. I. Ctenuchidæ. *Bull. & ann. soc. ent. Belgique* 84: 231-276, 3 pls.

....., 1949a. Over de Phylogenie van de Thyretidæ fam. nov. (Lepidoptera). *Natuurwet. Tijdschr.* 30: 3-10, 1 pl., 1 fig.

....., 1949b. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. II. Thaumetopœidæ. *Biol. Jaarb.* 16: 195-205, 5 figs.

....., 1950a. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. III. Dioptidæ. *Bull. & ann. soc. ent. Belgique* 86: 67-86, 2 pls.

....., 1950b. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. IV. Notodontidæ. *Biol. Jaarb.* 17: 66-111, 12 figs.

....., 1950c. Sur la classification et la phylogenie de la superfamille Notodontoidea (F. d'Almeida) Kiriakoff. *Bull. & ann. soc. ent. Belgique* 86: 23-255.

....., 1950d. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. V. Position systématique de quelques genres des Arctiidæ. *Lambillionea* 50: 62-73, 4 figs.

....., 1951a. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. VI. Nyctemeridæ. *Bull. & ann. soc. ent. Belgique* 87: 106-129.

....., 195lb. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. VII. Lithosiidæ. *Biol. Jaarb.* 18: 53-76, 7 figs.

....., 1951c. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. VIII. Cocytiidæ. *Ent. Berichten* 13: 381-382.

....., 1952a. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. IX. Arctiidæ. *Bull & ann. soc. ent. Belgique* 88: 26-50, 7 figs.

....., 1952b. Les organes tympaniques des lépidoptères comme caractère systématique et phylogénétique. *Lepid. news* 6: 7-12, 5 figs.

....., 1953. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. X. Hyblæidæ. *Bull. & ann. soc. ent. Belgique* 89: 258-263, 1 fig.

....., 1955. Onderzoekingen over de Gehoororganen bij Vlinders met Betrekking tot de Classificatie. XI. Agaristidæ. *Verh. Kon. Vlaamsche Akad. Wet. Lett. België* 47: 70 pp., 39 figs.

....., 1956a. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. XII. Lymantriidæ. *Bull. & ann. soc. ent. Belgique* 92: 168-199, 14 figs.

....., 1956b. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. XIII. Groupe d'*Epicoma* Hübner. *Biol. Jaarb.* 23: 218-227, 5 figs.

....., 1958. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. XIV. Nolidae. *Biol. Jaarb.* 26: 69-75, 6 figs.

....., 1960. Recherches sur les organes tympaniques des lépidoptères en rapport avec la classification. XV. Hypeninæ et Herminiinæ. *Biol. Jaarb.* 28: 140-153, 7 figs.

Luh, Chin-Jen, 1936. The skeletal structures of the tympanum of Arctiidæ (Lepidoptera). Dept. Ent., N. Y. State College of Agric., Cornell Univ., Ithaca, N. Y. (excerpt).

Richards, A. Glenn, Jr., 1933. Comparative skeletal morphology of the noctuid tympanum. *Ent. Americana* (n.s.) 13: 84 pp., 20 pls.

Sick, H., 1935. Die Bedeutung der Tympanalorgane der Lepidoptera für die Systematik. (*Verh. Dtsch. zool. Ges.* 37) in *Zool. Anz., Suppl.* 8: 131-135.

....., 1940. Beitrag zur Kenntnis des Dioptidæ, Notodontidæ und deren Verwandtschaftsbeziehungen zueinander. *Zool. Jahrb.* (*Anat.*) 66: 263-290, 29 figs.

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